

The role of prey mobility in the population ecology of the nudibranch *Cuthona nana* (Gastropoda: Opisthobranchia)

Nadine C. Folino*

Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824 U. S. A.

Abstract: The aeolid nudibranch *Cuthona nana* (Alder and Hancock, 1842) was studied in relation to its specific prey, the hydroid, *Hydractinia polyclina* (Agassiz, 1862). In this predator-prey association, the predator's spatial patterns and behavior, along with prey mobility, could play an important role in maintaining this nudibranch population. The seasonal abundances of *C. nana* documented in this study agree with the sub-annual life cycle previously presented. Both adult and juvenile nudibranchs were present on colonies during most months sampled in 1986-1988. The low prevalence of nudibranchs on hydroid colonies, the behavior of adult *C. nana* (leaving colonies periodically), regeneration in the hydroid, and prey mobility appear to be crucial in maintaining this unique species-specific, predator-prey association. Most nudibranch prey are non-mobile while *H. polyclina* grows on gastropod shells occupied by hermit crabs of the genus *Pagurus*. Adult *C. nana* repeatedly leave the hydroid colonies both in the field and laboratory to lay egg masses, while juveniles spend extended periods of time on the colony and leave only when they approach sexual maturity. The adult behavior of leaving colonies to lay egg masses does not severely jeopardize the newly hatched nudibranchs' probability of finding food. Hermit crab mobility is high and within a 24-hr period crabs frequently pass a given area containing juvenile nudibranchs. Juveniles encounter the hydroid's streaming gastrozooids sweeping over the substratum. *C. nana* undergoes non-pelagic lecithotrophic development from yolk-rich eggs with individuals hatching as crawling juveniles. The predator-prey dynamics between *C. nana* and mobile colonies of *H. polyclina* are similar to those seen in host-parasite associations.

Key words: Hydroidea, Nudibranchia, population ecology, predator-prey, Aeolidoidea, Hydractinia

Few studies describe nudibranch predator population parameters in relationship to their prey (Potts, 1970; Harris, 1973; Todd, 1979, 1981, 1983). Most nudibranch population studies show seasonal population fluctuations and suggest that physical (temperature, wave action) or biological factors (prey availability, competition, predation) control such fluctuations (reviews: Harris, 1973; Todd, 1981, 1983). Aeolid nudibranchs (Gastropoda, Opisthobranchia) often are abundant in seasonal hydroid communities; the communities are sessile and seasonal due to heavy grazing by predators, or because of changes in temperature (Miller, 1961; Thompson, 1964; Fager, 1971; Clark, 1975; MacLeod and Valiela, 1975; Nybakken, 1978; Harris and Irons, 1982).

Unlike most hydroids, the colonial gymnoblastic hydroid *Hydractinia polyclina* (Agassiz, 1862) (formally known as *H. echinata* Fleming, 1828; Buss and Yund, 1989) is a persistent food source throughout the year and is a mobile prey. In the southern Gulf of Maine, *H. polyclina* grows primarily on shells occupied by the hermit crab *Pagurus acadianus* (Benedict, 1901) and less frequently on

the shells occupied by *P. arcuatus* (Squires, 1964). No studies have considered how hermit crab movement affects the accessibility of predators to epifaunal prey organisms on their shells. Knowing the probability of a hermit crab passing a given area on the benthos would provide information on prey availability for a predator and how that could impact the population ecology.

The aeolid nudibranch *Cuthona nana* (Alder and Hancock, 1842) (Aeolidoidea) is a hermaphroditic opisthobranch that feeds specifically and exclusively on *Hydractinia polyclina*. Sexually mature *C. nana* leave crab shells bearing hydroid colonies to mate and lay egg masses (Rivest, 1978; Folino, 1993). Relocating a colony for further feeding is a unique challenge for *C. nana* compared to other hydroid feeders. Non-pelagic lecithotrophic larvae hatch and are picked up by the gastrozooids (feeding polyps) of the passing hydroid colony (Rivest, 1978). The movement of the hermit crab is therefore important in bringing the prey, *H. polyclina*, to the slow-moving predator, *C. nana*.

This study documents the localized dynamics of *Cuthona nana* and its prey off of the coast of Maine and expands on shorter previous studies by Rivest (1978) and Folino (1985). The purpose of this study was three-fold: (1)

*Present Address: Biology Department, Wheaton College, Wheaton, Illinois 60187-5593 U. S. A., Nadine.C.Folino@wheaton.edu

to describe the population structure of *C. nana* by documenting nudibranch densities, distributions, and size frequencies on shells with colonies from May 1986 to May 1988 at Gosport Harbor, Maine; (2) to compare juvenile and adult movements on and off *Hydractinia polyclina* colonies; *i. e.* how this behavior affects the location of mobile prey on hermit crab shells; and (3) to estimate prey accessibility for *C. nana* by determining the degree of movement by hermit crabs with hydroids on their shells within a given area. Does crab mobility have an impact on prey availability which could regulate *C. nana* populations?

METHODOLOGY

Collection of animals

Specimens of *Cuthona nana* and colonies of *Hydractinia polyclina* were collected using SCUBA from Gosport Harbor (Haley Cove, Isles of Shoals, Maine), ca. 9.5 km off the New Hampshire coast (42°59' N; 70°36' W). Hermit crabs occurred mainly in the sandy portions of the harbor at depths of 5-10 m.

Population data for *Cuthona nana* was obtained from 23 monthly collections (May 1986 to May 1988) of 21 to 90 hermit crabs, each with colonies covering ca. 100% of the available shell surface. The coverage is approximate because the shell scrapes the bottom when the crab crawls, preventing colony growth. Hydroid-covered shells were placed in individual containers in the field to insure that nudibranchs remained on their original colonies. The containers were either plastic jars (125 ml) or mesh containers (Toby Tea-boys, mesh size ca. 164 μ m; Daniel Peikin Company, Silver Spring, Maryland). Although efforts were made to collect shells of various sizes with *Hydractinia polyclina*, larger shells were more visible, creating a sampling bias towards larger shells. Colonies were later examined for nudibranchs using a dissecting microscope.

Nudibranch population structure

For each hydroid-covered shell (therefore for each hydroid colony) the density of nudibranchs and their sizes were recorded. The number of *Cuthona nana* was used to determine the abundance of nudibranchs per colony. Indices of dispersion were calculated to determine the degree of aggregation of nudibranchs on colonies. The dispersion pattern was further analyzed by making comparisons to a negative binomial distribution (Ludwig and Reynolds, 1988; Krebs, 1989). Co-occurrence of nudibranchs was determined by scoring the size of each nudibranch collected on a *Hydractinia*-covered shell versus the number of conspecifics present on the same colony.

Individuals were scored as being alone, paired, or with three or more nudibranchs. The nudibranchs were divided into non-reproductive (< 9 mm) or reproductive (> 9 mm) groups based on anatomical and behavioral aspects of reproduction (Rivest, 1978; Folino, 1993).

To determine if colony size affected the number of nudibranchs present on a colony, correlation coefficients were calculated for nudibranch number and colony size for each month sampled. The surface area of a given shell was determined using its linear dimensions following a technique modified (see Folino, 1993) from that used by Shenk and Karlson (1986). Colony size was then estimated from shell surface area. In months when there were small numbers of colonies with nudibranchs present, the data were pooled.

Histograms of nudibranch length frequencies were used to examine the age-class structure by month and were compared for yearly differences using Kolmogorov-Smirnov tests (Sokal and Rohlf, 1981). Monthly size-class histograms (See Folino, 1989) were summarized by grouping individuals into non-reproductive individuals (< 9 mm) and reproductive individuals (> 9 mm) as previously mentioned.

Measuring nudibranch movement

A laboratory experiment was designed to determine differences between juvenile and adult *Cuthona nana* in movement on and off hydroid-colonized hermit crab shells. Hermit crabs were maintained in trays (76 x 64 x 9 cm) filled with sand from Gosport Harbor. Beetags (from Chr. Graze KG, West Germany) were used to label shells so that individual colonies could be assessed for the presence or absence of nudibranchs. Because nudibranchs are difficult to tag, tagging the shells was a way of monitoring nudibranch movement (*i. e.* whether a nudibranch was present or absent since the previous observation). Each tray contained ten tagged hermit crabs and four nudibranchs. Tray densities were chosen from the highest field densities recorded from cofferdam samples taken in May 1987. [A cofferdam is a metal cylinder (0.153 m²) placed on the benthos to prevent hermit crabs in the enclosed area from escaping before being counted.]

Two trials with two replicate trays were conducted using adult nudibranchs of 12-20 mm. Each adult trial lasted 12 days, and the shells were examined twice daily for the presence or absence of nudibranchs, once in early morning and once in late afternoon to account for night and day activity. Nudibranch movement was measured by calculating the mean number of moves (or change in nudibranch number) on or off a colony per day. A similar experiment was conducted using juvenile (2-4 mm) nudibranchs. One trial of juveniles consisting of four replicated trays was conducted for 21 days.

Measuring hermit crab mobility

Hermit crab mobility was estimated by deploying pitfall traps (Uetz and Unzicker, 1976) on the bottom of Gosport Harbor to sample crabs passing a given area in a 24-hr period. The traps were plastic containers ca. 11 cm in diameter and 15 cm deep. Two grids (each measuring 5 x 5 m) were used to randomly position 20 pitfall traps; holes for the containers were dug in the sand using an airlift. Each container was marked with a numbered flag to insure relocation. Trials were performed monthly from January through May 1988; April was excluded due to rough seas. A given trial consisted of leaving the traps uncovered for 24 h from mid-morning to mid-morning. Traps were emptied and crabs from a given trap were placed in a mesh bag. The number of crabs caught per trap and the presence or absence of *Hydractinia polyclina* colonies on the shells of each crab were recorded. Traps were covered between trials; a few traps became filled with sand and could not be relocated during two of the four trials.

RESULTS

Nudibranch densities

Monthly collections of crabs with hydroid-covered shells provided seasonal estimates for the population of *Cuthona nana* at Gosport Harbor. The mean number of nudibranchs per colony collected from May 1986 to May 1988 demonstrated seasonality of densities, with maxima in April, May, and August, and minima in October and November (Fig. 1). The greatest mean number per shell occurred in May 1987 (2.380; SE = 0.386) and most of those individuals (87%) were < 4 mm in length.

The percentage of hydroid-covered shells with one

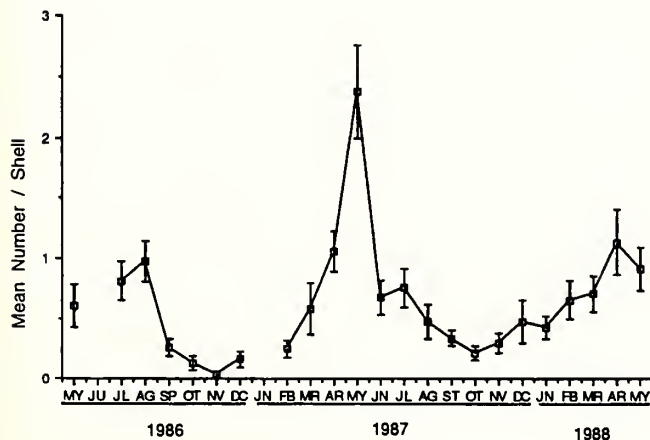


Fig. 1. The mean number of *Cuthona nana* per hydroid-covered hermit crab shell for each month sampled from May 1986 to May 1988. The bar for each mean represents standard error.

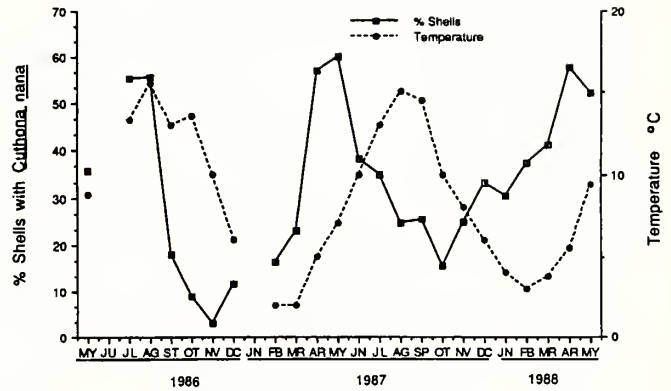


Fig. 2. The percentage of hermit crab shells covered with *Hydractinia polyclina* having one or more *Cuthona nana* present, plotted with temperature.

or more *Cuthona nana* fluctuated over the 23 mo sampled. The greatest percentages of occupied shells for 1986 were in July and August with 55% and 56%, respectively, while April and May showed the greatest percentage of colonies with nudibranchs in 1987 and 1988 (Fig. 2). The percentage of shells with nudibranchs declined in late summer and early fall in 1986 and 1987, and began to increase in November and December in both years. The percentage of shells with nudibranchs increased in the colder months suggesting an increase in population numbers (Fig. 2).

Nudibranch distributions

Nudibranchs demonstrated an aggregated rather than random dispersion pattern on colonies for all months sampled; tests could not be performed for October, November, and December 1986, and November 1987 because of small sample sizes (Table 1). All indices of dispersion (variance/mean number of nudibranchs per colony ratios) were greater than 1.0, providing evidence for aggregated distributions (Krebs, 1989) (Table 1). A large number of colonies had no nudibranchs, and the ranges of distribution varied by month. In May 1987 and April 1988 a greater range of frequencies was observed; some colonies had as many as 11-19 nudibranchs per colony. Eight out of nineteen months fit the negative binomial distribution indicating strong patterns of aggregation during those months (Table 1).

Numbers of nudibranchs and colony size were not significantly correlated for any of the years sampled (1986: $r = -0.080$, $N = 84$; 1987: $r = 0.068$, $N = 241$; 1988: $r = 0.015$, $N = 128$, $p > 0.50$ in all cases). Correlation coefficients were also determined for shell size (*i. e.* colony size for completely covered shells) and the number of non-reproductive nudibranchs to test the assumption that larger colonies acquired more juvenile nudibranchs (from the benthos). Again, no significant correlations were obtained

Table 1. The indices of dispersion (variance:mean ratios) and the negative binomial distribution statistics for the number of hydroid-covered shells with 0-19 *Cuthona nana* from May 1986 to May 1988. (k, exponent of the negative binomial distribution; N, number of sample units or hermit crabs; P, probability for the calculated X^2 values of the negative binomial distribution; S^2/\bar{X} , variance to mean ratio; $\bar{X} \pm SE$, mean plus or minus standard error; X^2 , goodness-of-fit of the negative binomial distribution; *, significant fit to the negative binomial distribution).

	MONTH	S^2/\bar{X}	N	$\bar{X} \pm SE$	k	X^2	P (df = n - 3)
1986	MAY	1.50	28	0.607 ± 0.181	0.73	1.45	P < 0.100 (1)
	JUL	1.25	38	0.816 ± 0.164	16.0	9.17	P < 0.010 (2)*
	AUG	1.23	45	0.978 ± 0.164	2.0	0.91	P < 0.250 (2)
	SEP	1.48	84	0.262 ± 0.068	0.37	1.54	P < 0.100 (1)
	OCT	1.56	68	0.132 ± 0.055	---		
	NOV	1.00	33	0.030 ± 0.030	---		
	DEC	1.46	61	0.164 ± 0.063	---		
1987	FEB	1.55	73	0.247 ± 0.072	0.30	1.28	P < 0.250 (1)
	MAR	3.97	52	0.519 ± 0.199	0.21	13.17	P < 0.025 (6)*
	APR	1.76	63	1.060 ± 0.172	2.00	19.49	P < 0.001 (5)*
	MAY	5.64	90	2.380 ± 0.386	0.54	19.79	P < 0.100 (16)
	JUN	1.83	63	0.683 ± 0.141	0.79	1.97	P < 0.250 (2)
	JUL	3.03	87	0.759 ± 0.163	0.44	8.44	P < 0.100 (6)
	AUG	2.96	65	0.477 ± 0.147	0.28	14.70	P < 0.010 (6)*
	SEP	1.34	98	0.337 ± 0.068	1.10	2.94	P < 0.100 (2)
	OCT	1.47	83	0.217 ± 0.062	0.62	0.25	P < 0.500 (1)
	NOV	1.04	44	0.295 ± 0.083	---	---	
	DEC	1.40	21	0.476 ± 0.178	1.30	0.88	P < 0.250 (1)
	1988	JAN	1.26	56	0.429 ± 0.098	1.10	0.695
FEB		2.38	59	0.661 ± 0.163	0.71	18.56	P < 0.001 (5)*
MAR		1.77	56	0.714 ± 0.150	0.93	6.70	P < 0.005 (1)*
APR		3.62	57	1.140 ± 0.269	1.34	137.8	P < 0.001 (9)*
MAY		9.33	63	0.921 ± 0.181	1.76	167.7	P < 0.001 (7)*

(1986: $r = -0.098$, $N = 60$; 1987: $r = 0.086$, $N = 160$; 1988: $r = -0.010$, $N = 84$).

Chi-square analyses indicated no significant pattern for the distribution of reproductive adults being alone, paired, or with three or more individuals on a given colony ($X^2 = 4.41$, $P < 0.111$, $df = 2$, $N = 95$). Of the sexually mature animals on shells, approximately equal numbers were found alone, paired, or with three or more nudibranchs. The > 3 category showed the lowest percentage (Fig. 3). On the other hand, non-reproductive nudibranchs showed a significant pattern of aggregation ($X^2 = 92.88$, $P < 0.0001$, $df = 2$, $N = 768$), with 49% of the animals occurring in groups of three or more on a colony. Significant differences existed in the three categories between the reproductive and non-reproductive individuals, suggesting behavioral differences between juvenile and adult nudibranchs (G-test, $p < 0.001$).

Size Frequencies

Mean size of *Cuthona nana* on colonies varied for each month over the 2.5 yr sampling period (Fig. 4). Mean size increased from July to October for both 1986 and

1987. In all three years, more non-reproductive than reproductive individuals were present each month (Fig. 5). Reproductive adults were present on colonies in all months for 1986 except July and November, and were absent in August, November, and December 1987 (Fig. 5). This does not mean that adults were absent from Gosport Harbor, but they were not present on the colonies collected. Adults were present on colonies in all five of the months sampled in 1988. The percentage of adults in the summer months varied for 1986 and 1987 and decreased in late summer and early fall, followed by an increase in October for both years.

Nudibranch movement on and off of colonies

The results of nudibranch movement on and off of *Hydractinia polyclina* colonies indicated that adults were more active; they averaged one to two moves on or off crabs with colonies per day (Fig. 6). These numbers are most likely underestimates, because more excursions from colonies could have occurred within the time of census. Adults (12-20 mm) were more active than juveniles in both trials; often during the adult trials, animals were observed

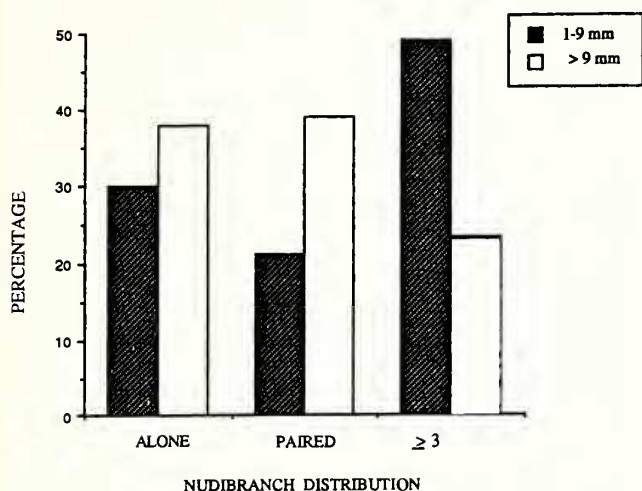


Fig. 3. The percentage of non-reproductive (1-9 mm) and reproductive (> 9 mm) *Cuthona nana* scored as solitary, paired, or with three or more individuals on a hydroid-covered hermit crab shell from May 1986 to May 1988. Chi-square tests indicated a significant difference among the three categories for non-reproductive animals ($P < 0.0001$, $df = 2$) and non-significant differences for reproductive individuals.

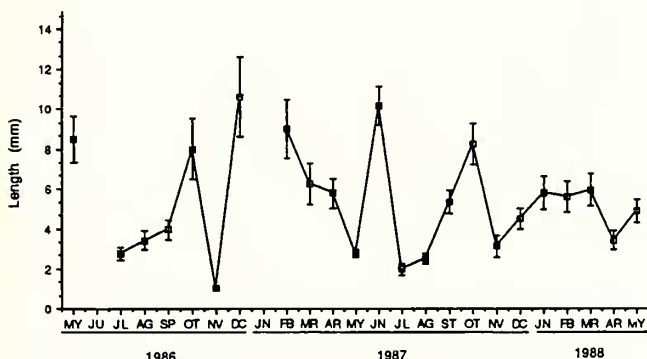


Fig. 4. Mean size of *Cuthona nana* on hydroid-covered hermit crab shells for each month of collection. The bar for each mean represents standard error.

mating and laying egg masses on rocks and the sides of the sea water tables. No egg masses were laid on colonies of *H. polyclina* during the experiment. Juvenile nudibranchs (2-4 mm) did not leave shells covered with *H. polyclina* under the experimental conditions employed (Fig. 6). No juvenile nudibranchs left the colonies where they were initially placed in any of the four trays.

Hermit crab mobility

Considerable hermit crab activity occurred in a 24-h period in view of the fact that this experiment was conducted during the colder months of the year. In 24-h, the mean number of crabs caught per pitfall trap ranged from 15-26 (Jan.: 15.4 ± 10.2 SD, $N = 308$; Feb.: 21.3 ± 11.0 SD, $N = 383$; Mar.: 15.0 ± 11.0 SD, $N = 251$; May: 26.7 ± 13.9 SD,

$N = 533$). The mean number of crabs caught that were colonized with *H. polyclina* ranged from 3-8 (Fig. 7). On average, six crabs with *H. polyclina* passed a given area during a 24-h period. This supports the probability that crabs with hydroids were likely to pass by a given nudibranch within a 24-h period. The number of shells with (and without) *H. polyclina* increased from March to May. The four months sampled were during the time of year with low crab and hydroid densities, thus providing conservative estimates (Grant, 1963; Rivest, 1978).

DISCUSSION

Nudibranch population patterns

The population patterns of *Cuthona nana* at Gosport Harbor indicate a sub-annual life cycle during which the species undergoes several generations in a year (Miller, 1962; Thompson, 1964; Harris, 1973, 1975; Todd, 1981, 1983). The results of this study paralleled those of Rivest (1978) and Folino (1985) but also provided information on summer abundances during months when data had not been previously obtained. The presence of juveniles throughout all months sampled, in conjunction with adults present in the summer and fall and continuous egg-laying, indicates the existence of overlapping generations.

Although most species of nudibranchs with several generations per year feed on seasonal prey (Miller, 1962; Clark, 1975; Harris, 1973; Todd, 1981, 1983), two species, *Phestilla* sp. and *Cuthona nana*, do not (Harris, 1975; Rivest, 1978, and Folino, 1989, respectively). Prey availability for *C. nana* depends upon crab location; although most crabs migrate to deeper water during colder months, there are still crabs present in shallower water with colonies available for food during the winter (Rivest, 1978; Folino, 1989). Thus, the population of *C. nana* at Gosport Harbor is able to persist throughout the year due to the presence of crabs with colonies.

Partial predation

This nudibranch-hydroid association is an example of partial predation on colonial organisms, a phenomenon that has received increased attention in recent years for both plants and animals (Jackson, 1985; Coates and Jackson, 1985; Harper, 1985; Harvell and Suchanek, 1987; Todd and Havenhand, 1989). *Hydractinia polyclina* regenerates when damaged by predators (Christensen, 1967; Sutherland and Karlson, 1977; Karlson, 1978; Buss *et al.*, 1984; Folino, 1985; McFadden, 1986). Based on previous grazing rates (Folino, 1985, 1993), a large *Cuthona nana* could graze approximately one-quarter (23%) of an average-sized colony in less than a 24-h period and leave a substantial portion for continued growth. These estimates of

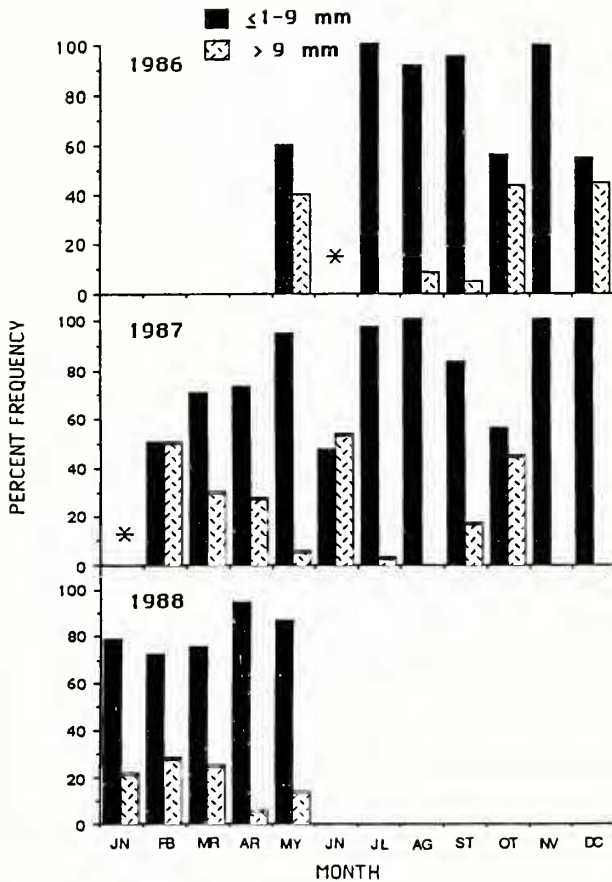


Fig. 5. Percent frequencies of non-reproductive (1-9 mm) and reproductive (> 9 mm) *Cuthona nana* collected from May 1986 to May 1988. (*, sampling not possible due to rough seas).

grazing consider only one large nudibranch on a colony; obviously two or more large animals would do more damage. Even so, grazing does not completely decimate the prey as a food source. Furthermore, the majority of colonies collected did not support nudibranchs; the percentage of colonies (or shells) with nudibranchs did not exceed 60% (Fig. 2). This again suggests that *C. nana* is not limited by prey availability.

Laboratory data on colony growth and regeneration are ambiguous. In small colonies, predator consumption rates (large *Cuthona nana* eat 200-500 polyps in a 24-h period at 12°C; Folino, 1993) can outstrip hydroid growth. However, growth rates also increase with temperature and colony size (McFadden *et al.*, 1984; Folino, 1985) suggesting that larger colonies produce polyps at a rate closer to that of polyp removal by predators.

The presence of chitinous spines on most colonies of *Hydractinia polyclina* in this study prevents complete removal of polyps by *Cuthona nana* (see Folino, 1993), a situation analogous to that seen in bryozoan zooids where spines reduce nudibranch grazing rates (Yoshioka, 1982;

Harvell, 1984). Polyps that have been partially eaten can clearly regenerate (Folino, 1993). Therefore, *C. nana* do not decimate prey as is true in other nudibranch-hydroid associations (Clark, 1975; Todd, 1981, 1983).

Nudibranch distributions and movement

The aggregation of sexually immature *Cuthona nana* on *Hydractinia polyclina* (and lack of aggregation of reproductive individuals) differs from studies of other species in which aggregation occurs in both sexually mature and immature individuals (Miller, 1962; Clark, 1975; Todd, 1981, 1983). Potts' (1970) work with *Onchidoris bilamellata* (Linné, 1767) [= *O. fusca* (Müller, 1776)] suggested that the nudibranchs probably remain on the rock where they initially settled because ample food and mates are available. Field observations by Todd (1978a, 1979) for *O. muricata* (Müller, 1776) and *O. bilamellata* showed increased aggregation during the breeding season, suggesting that animals stay within an area where food and other sexually mature individuals are present. The distribution pattern seen in *C. nana* populations could be produced by the behavior of the nudibranchs. As juveniles, they hatch from eggs laid on rocks, mussel shells, and *Chondrus* (Rivest, 1978; Folino, 1993). Juveniles appear to be picked up by *H. polyclina* gastrozooids that sweep along the ocean bottom, and they remain on the colony until sexually mature. Adults leave hydroid colonies and follow mucus trails to find potential mates, as do other mollusks (Lowe and Turner, 1976; Todd, 1978b, 1979; Gerhart, 1986; see review: Hadfield and Switzer-Dunlap, 1984). During the peak reproductive periods for *C. nana* from April through September, Rivest (1978) and Folino (1989)

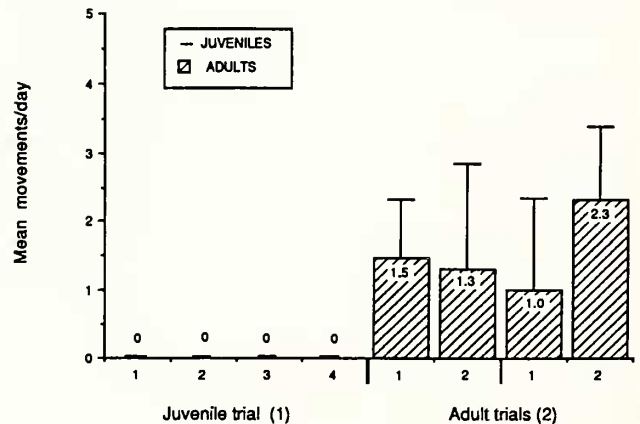


Fig. 6. Nudibranch movement on and off of *Hydractinia* colonies. One trial with four replicates (left) indicating that juvenile *Cuthona nana* (2-4 mm) did not leave colonies during a 21-d period. Alternatively, adults (12-20 mm) moved on and off an average of 1-2 times per day (two 12-d trials, right). The bar for each mean represents standard deviation.

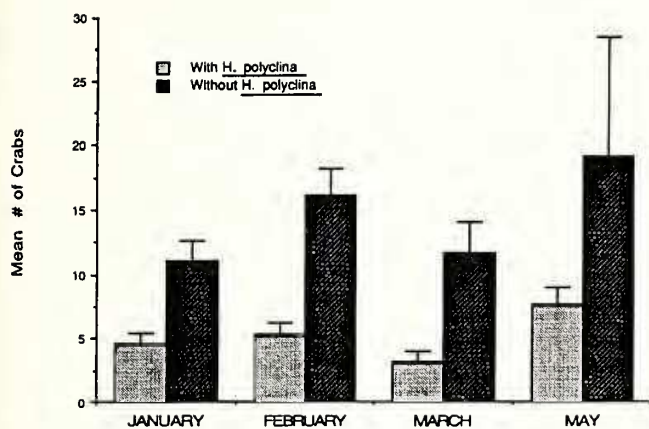


Fig. 7. Mean number of hermit crabs caught in pitfall traps in a 24-h period during four months in 1988. Twenty traps were sampled in January and May while 18 and 17 traps were sampled in February and March, respectively. The bar for each mean represents standard deviation.

observed adult *C. nana* more frequently crawling on the bottom of Gosport Harbor. Mating does occur on the hydroid colonies, but occurs more often off of them (Harris *et al.*, 1975; Rivest, 1978; Folino, 1985, 1989). The results of the laboratory nudibranch movement experiment support these field observations of nudibranch behavior (Fig. 6). *C. nana* behavior differs from those of the dorid nudibranchs, *Onchidoris* spp., where encounters with mates are enhanced due to aggregation near stationary prey (Potts, 1970; Todd, 1978a, 1979). Movement of adult *C. nana* off of its mobile prey increases the chances of encountering mates.

The life history of *Cuthona nana* differs from those of other hydroid-feeding aeolids. In most species, larvae are planktonic, and settle on sessile prey for growth through sexual reproduction (Todd, 1981, 1983). In contrast, *C. nana* at Gosport Harbor lacks a planktonic veliger and exploits a mobile prey. Once picked up by a passing crab, juveniles feed on basal mat tissue until they reach ca. 5-6 mm, when they are large enough to consume polyps (Folino, 1993). Furthermore, crab mobility could help distribute juvenile nudibranchs over several colonies preventing over-predation of some (especially small) colonies (Rivest, 1978). This decreases the degree of grazing on an individual colony (Folino, 1993) and could also promote genetic variation in the population by 'mixing up' cohorts.

Cuthona nana behavior is similar to that of plant bugs (Miridae) (Price, 1980). Adult plant bugs are large ectoparasites and are mobile, whereas the immature stages spend all of their time on a single host. Juvenile *C. nana* showed a similar behavior and did not switch colonies in the laboratory. Thus differences exist between adult and juvenile residence time, which affect the degree of grazing on the prey. This behavior in *C. nana* seems to parallel the

prudent parasite model because partial (rather than total) consumption of the prey is important to the predator's survival (Holmes, 1983).

Hermit crab movement

Cuthona nana at Gosport Harbor do not lay egg masses on colonies of *Hydractinia polyclina*, but rather on the ocean floor. Because hermit crab movement will bring prey to juveniles on the bottom, adult *C. nana* at Gosport Harbor do not jeopardize the juveniles' probability of finding food by depositing egg masses off of the colonies (Rivest, 1978; Folino, 1993). Non-planktonic development in the *C. nana* population at Gosport Harbor could actually be an adaptation to a mobile prey and to trophic stability (Clark and Goetzfried, 1978). With yolk present at metamorphosis, juveniles can survive for up to ten weeks without feeding at 4°C (Rivest, 1978), which is ample time for a crab to bring food (Fig. 7). The results of the pitfall experiment indicate that crabs with colonies of *H. polyclina* are fairly active over a 24-h period and provide sufficient opportunities for prey encounters. This experiment in conjunction with the monthly collections of shells with colonies indicates a non-seasonal food supply for *C. nana*. *Hydractinia* is continuously available in Gosport Harbor, especially at the time of metamorphosis, allowing for non-planktonic development.

There are several similarities between the life history of *Cuthona nana* and that of a parasite (Price, 1980; Strand and Obrycki, 1996); such similarities shed insight on the maintenance of *C. nana*'s population. *C. nana* is much like a parasite in being a specialist on *Hydractinia polyclina*. The phenomenon of juveniles being picked up by their prey is similar to a host-parasite relationship, such as is seen with intermediate stages of parasitic trematodes, flukes, or hookworm larvae (Cheng, 1970). Juvenile *C. nana* ("parasites") on the ocean floor are picked up by prey ("host") passing by; alternatively adults can conceivably crawl onto a colony while a crab is temporarily stationary and is filter feeding (Gerlach *et al.*, 1976; Rivest, 1978; pers obs.). Furthermore, similar to a parasite (Price, 1980), *C. nana* is not a fast-moving predator "chasing" mobile colonies of *H. polyclina*. Adult *C. nana* can crawl onto a colony while a crab is stationary or onto a colony without a crab in the shell. Thus, the movement and egg-laying behavior of *C. nana* adults at Gosport Harbor along with the hydroids' ability to regenerate and the mobility of the prey on the crab shells all contribute to the persistence of prey availability throughout the year. Prey availability is very important in determining the population patterns of a specialized predator like *C. nana*. These factors allow for the sub-annual life cycle and perhaps non-planktonic development of *C. nana* with prey not being the limiting factor for the population ecology of this prey-specific nudibranch.

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